THE BIOLOGY OF *ASCIDIA NIGRA* (SAVIGNY) V. SURVIVAL IN POPULATIONS SETTLED AT DIFFERENT TIMES OF THE YEAR

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In previous papers one of us has reported on certain aspects of the biology of populations of the tropical ascidian *Ascidia nigra* with particular reference to reproduction, growth and survival in Jamaica (Goodbody, 1961a, 1962, 1963a, 1963b, 1965). Settlement of larval *Ascidia nigra* has been shown to go on throughout the year indicating that reproduction must be continuous within the whole population. Settlement data are based on the appearance of young ascidians either within existing populations or on test plates and they show marked variability with a tendency for larger numbers of new animals to appear in the winter than in summer. This variability could be due to increased egg production or better survival in the winter months of embryos, larvae or later stages of the ascidian. Studies on egg production are difficult to achieve and at present it is only possible to examine aspects of survivorship. Goodbody and Fisher (1974) have reported on survival of embryos and the present paper is concerned with the question of seasonal survival of juvenile and adult populations of ascidians.

During the first few weeks of life after metamorphosis of the larva there is a great variation in survivorship and Goodbody (1963a) illustrated three basic types of survival curve representing populations which left no survivors, about 3% survivors and about 15% survivors after six weeks of life. Goodbody assumed that these differences between populations were due to biotic effects of the surrounding community and suggested that interference by barnacles and algae was the most likely factor contributing to mortality. Once a population is established the mortality rate is low until about the fifteenth month after settlement following which it rapidly increases so that most animals are dead after about twenty months (Goodbody, 1962). These earlier studies were based on only a few experiments and provided no information on any seasonal differences in patterns of survivorship. If such differences were to exist they might have an important bearing on cycles of reproductive activity and the number of larvae available for settlement at any given time.

The work outlined in the present paper sets out to examine the following questions. (1) Is there any seasonal pattern of survivorship in juvenile populations which might account for the different densities of young animals appearing in older populations? (2) Is there any relationship between spawning peaks and survival of young ascidians which would suggest that spawning may be concentrated in periods of high survival? (3) How do abiotic and biotic factors in the environment affect survivorship? (4) Is there any evidence for seasonal differences in survival of adult populations which might suggest a selective advantage is given to individuals starting life at a particular time of the year?

The approach to answering these questions has followed two separate lines of investigation in two different sets of experiments. This is necessary because juvenile

ascidians are not visible to the naked eye in the first few weeks of life and must be reared under conditions in which their substrate can be removed for examination under a microscope. Such a substrate is unsuitable for the long term study of adult populations. It has not been possible to develop suitable techniques for studying natural spawning behaviour so that the second question remains unanswered. Changing patterns of juvenile survival have been studied over a period of two years by Gibson and illustrate some small but important seasonal differences. Attempts to correlate these changes with the associated biota have met with only limited success and suggest that barnacles and filamentous algae are less important than detritus and diatoms. Survivorship and expectation of life in a number of populations of adult ascidians, which started life at different times of the year, have been studied by Goodbody over a period of three years. The differences between these populations is examined in relation to both season and the nature of the associated sessile community.

METHODS

The methods used for studying juvenile populations were the same as those used in an earlier study. Larval ascidians were reared in the laboratory from artificial fertilizations and then allowed to settle on glass microscope slides. As soon as settlement was complete the slides were mounted in leucite (perspex) frames which were then suspended in the sea where natural sessile communities developed in association with the ascidians. Each frame carried six slides and was backed by black leucite so as to provide a dark background and permit growth on one side of the slide only. The frames could be removed from the sea at intervals and the slides individually examined under a microscope. For fuller details see Goodbody (1963a).

The method for obtaining and growing adult ascidian populations on "Tufnol" panels have already been outlined (Goodbody, 1962) and the specific details of the particular series of populations reported on here are given by Goodbody (1965).

TABLE I

Mean percentage survival of 32 pairs of populations of young specimens of Ascidia nigra *reared at four feet (1.2 meters) and at eight feet (2.4 meters) respectively below the surface of the sea. The data used in this table are drawn only from those instances in which populations commenced life simultaneously at four feet and at eight feet, thus providing matching pairs. Usually there were approximately 100 individuals in each population (see text).*

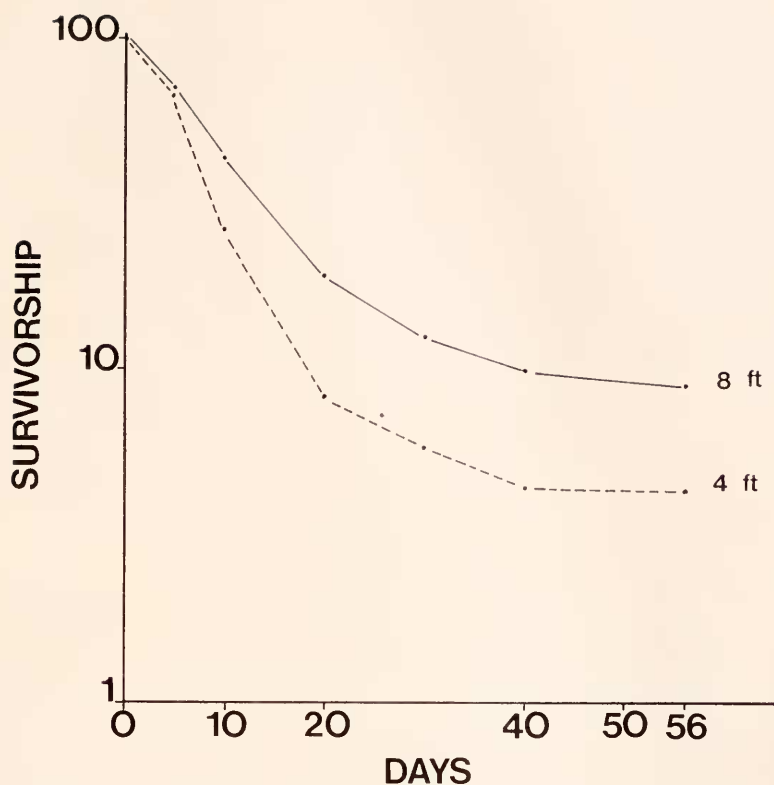| Day	5		10		20		30		40		56	
Depth (in feet)	4	8	4	8	4	8	4	8	4	8	4	8
Mean % Survival	67.3	69.8	26.7	40.3	8.3	19.1	5.8	12.5	4.4	9.9	4.3	8.9
S.D.	16.8	16.4	20	17.5	8.8	14.4	7.3	12.0	6.4	10.4	6.4	9.3
t	0.58		2.904		3.63		2.73		2.558		2.315	
P	0.6		0.005		0.001		0.010		0.02		0.02	

FIGURE 1. Mean survival in the first fifty-six days of life of all populations of *Ascidia nigra* reared at 4 feet (dashed line) and at 8 feet (solid line) below the sea surface. (See Table I).

Six separate populations were developed on panels immersed at two month intervals over a period of a year commencing in October 1959. Four panels were used for each population, two at four feet (1.2 meters) and two at eight feet (2.4 meters) below the sea surface. Each panel grew populations on both sides so that there are eight subpopulations within each main population. Panels were normally inspected at monthly intervals until October 1962 when the study was terminated.

Population C, which started life in February 1960, suffered serious damage and handling loss in the winter of 1960/61 and data from it are not used in this study on survival. Populations A and B (October 1959 and December 1959) suffered storm damage in the winter of 1960/61 and the data have been adjusted to enable survival curves to be drawn and an estimate made of the expectation of life. For details of the method of adjustment see Goodbody (1962). No observations were made in November 1960 during a period of exceptionally high winds. Figures given in the tables for this month are based on the mean values for October and December respectively. For details of the presentation of life tables and the calculation of the expectation of further life see Deevey (1947).

Survival in juveniles

Between January 1964 and December 1965 a total of 74 juvenile populations were studied, 35 reared at 4 feet (1.2 meters) and 39 at 8 feet (2.4 meters) below the surface of the sea. Each population was checked at intervals of about three days for a total duration of 56 days (8 weeks) after settlement of the larvae. Populations were selected which had as near to 100 individuals as possible. The mean population size at 4 feet was 89.6 (S.D. ± 13.1) and at 8 feet was 90.1 (S.D. ± 16.0). The plotted survival curves for each of these populations are deposited in the library of the University of the West Indies (Gibson, 1967) and no attempt is made to reproduce them here. All three types of survivorship recorded by Goodbody (1963a) occurred amongst these populations and as a general rule
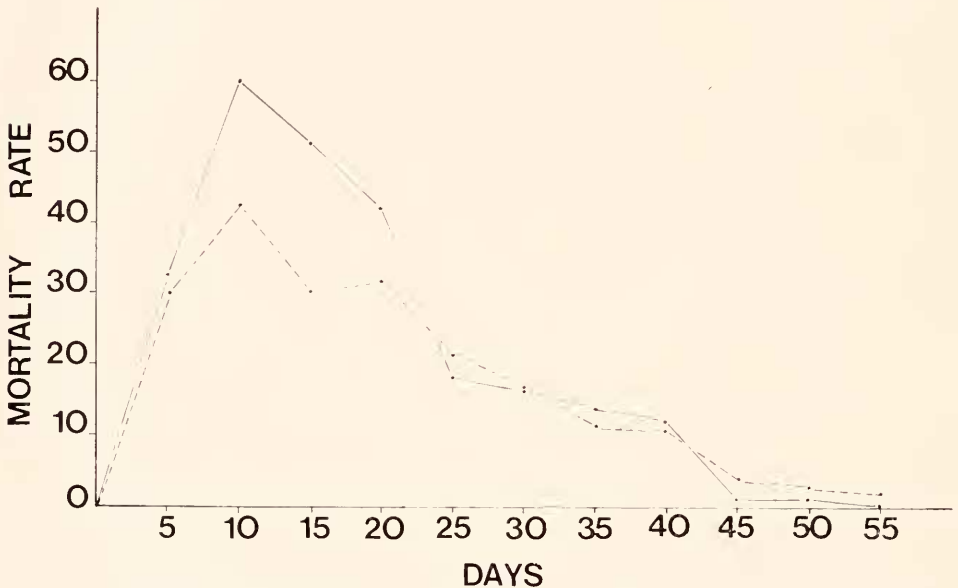

FIGURE 2. Mortality rate (100 q_x) of *Ascidia nigra* in the first eight weeks of life.

the pattern of survival is determined by the twentieth day after settlement (Gibson, 1967). The data in these survival curves have been used to construct both Table I and Figure 3.

Table I shows for 32 populations at 4 feet and 32 populations at 8 feet the mean percentage survival on the 5th, 10th, 20th, 30th, 40th, 50th and 56th day after settlement. These data can be used to construct the overall survival curves for 4 feet and 8 feet illustrated in Figure 1. This shows that in general more than 75% of ascidians have died before the nineteenth day when the black pigment is normally established (Goodbody, 1963a) and they confirm the contention that the first three weeks of life are the most critical in the life of the animal after settlement. This is illustrated more forcefully in Figure 2 where the data have been re-calculated

so as to show the mortality rate (*i.e.*, the number of animals dying in each interval of time per hundred alive at the beginning of that interval). A second and more important point, which emerges from Table I, is that there is a marked difference in mean survival between populations reared at 4 feet and at 8 feet and that this difference is significant from the 10th day onward. There may thus be some survival value in settling at the deeper level and the meaning of this is discussed later on.

In Figure 3 the percentage of each population surviving to the 56th day is plotted on a seasonal basis, the data above the base line being populations reared at 4 feet, those below the base line being reared at 8 feet. The dotted lines above and
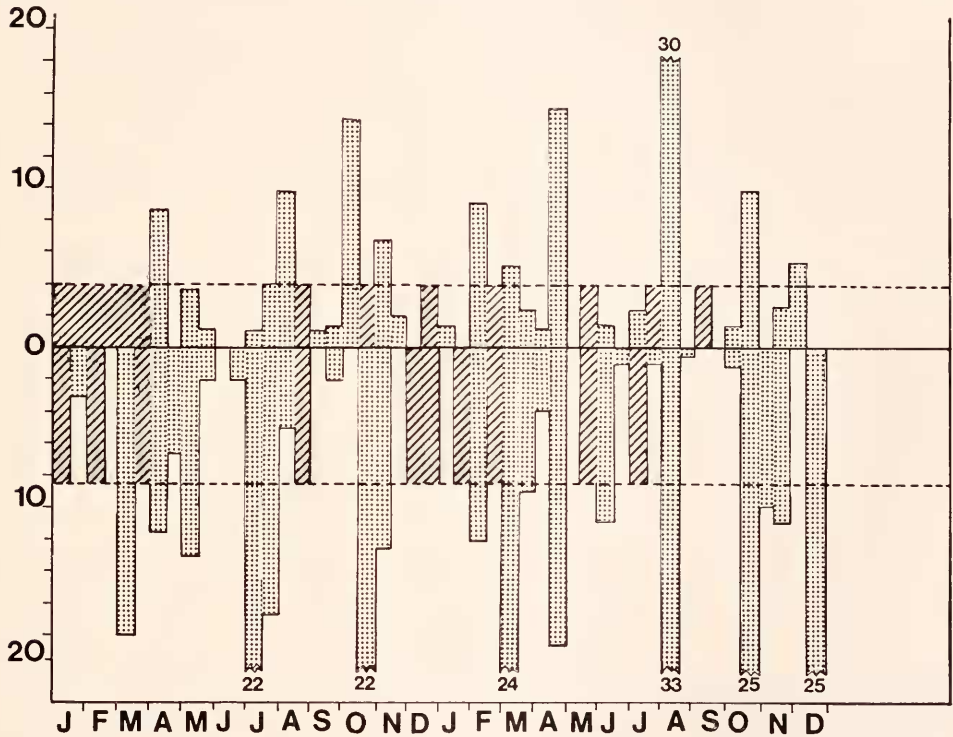

FIGURE 3. The percentage survival of ascidian populations on the fifty-sixth day after settlement when commencing life at different times of the year, shown as dotted blocks. Data above the base line refer to populations reared at 4 feet (1.2 meters) below the surface; data below the base line refer to populations reared at 8 feet (2.4 meters) below the surface. The dashed line indicates mean survival at each level. Cross-hatched blocks are periods in which no observations were made. Unfilled blocks indicate zero survival. For further explanation see text.

below the base line represent the two means of survival at the respective depths. Normally two populations were reared at each depth in each month and roughly two weeks apart. On certain occasions it was not possible to rear one or both groups and in order to differentiate these from periods of zero survival on the plot they are shown as lightly shaded bars extending to the mean.

It is apparent from this figure that there are two periods of poor survival in the year centered around the months of June and September respectively. There may also be a period of poor survival in December but the data for 1964 are too few to make this certain. Outside of these periods there is considerable variation in survivorship and it is apparent that high survival at 4 feet is usually matched by high survival at 8 feet, thus suggesting a general rather than a localized environmental effect on the populations.

Survivorship and expectation of life in adult populations

In an earlier paper (Goodbody, 1962) survivorship was plotted separately for each cohort of animals appearing in the first three months and these were treated as separate populations. The differences were small and in this paper only sur-
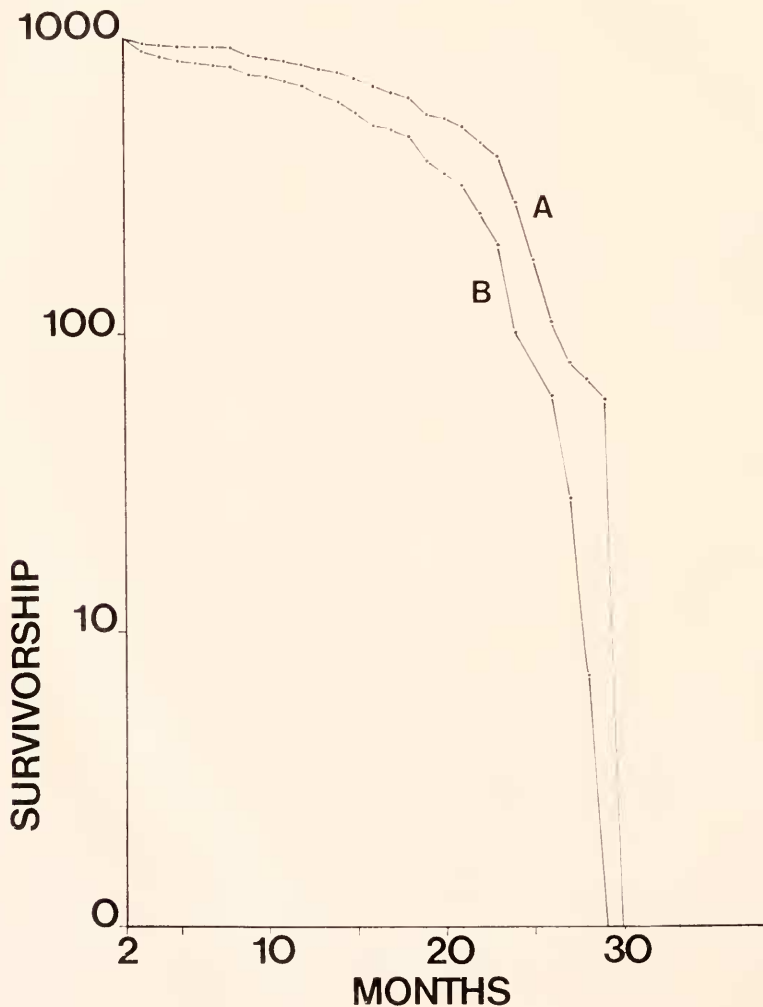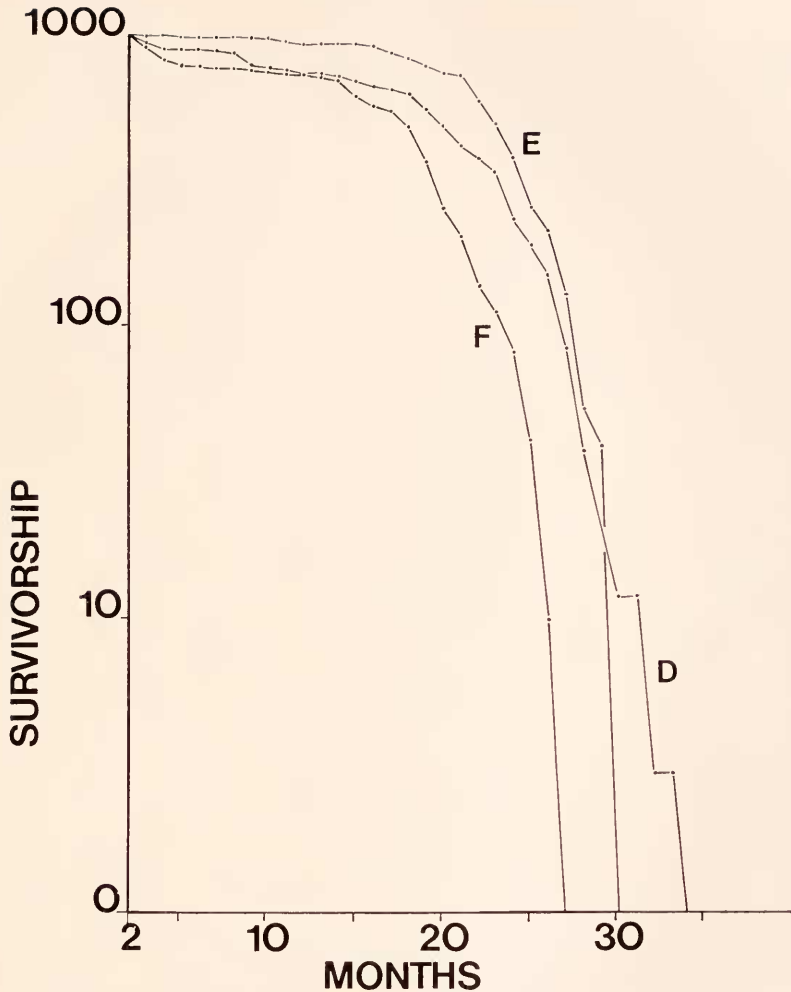
FIGURE 4. Survival curves for populations of *Ascidia nigra* settling at different times of the year. Graphs commence when animals are approximately two months old: (a) populations settled in October (A) and December (B); (b) populations settled in April (D), June (E) and August (F).

vival for the total number of adult *Ascidia nigra* present in each population two months after first immersion of the panels has been plotted.

Table II shows for each adult population the month of the year in which panels were first immersed, the total number of animals included in each population and the survival of these populations as cohorts of 1000 animals. It also shows the expectation of further life in each population in every month.

Survival curves for these five populations are shown in Figure 4. They confirm the picture given earlier (Goodbody, 1962) and show that irrespective of the time of year at which populations commence life the pattern of survival is the same.

TABLE II

Survivorship (l_x) *and expectation of further life* (e_x) *for five populations of* Ascidia nigra *settled at different times of year. Survivorship is expressed for cohorts of 1000 animals and the actual number of animals in each population is given in parentheses at the head of each column. Expectation of life is given in months.*

Population	A Oct (145)		B Dec (463)		D April (341)		E June (77)		F Aug (196)	
Time in Months	l_x	e_x	l_x	e_x	l_x	e_x	l_x	e_x	l_x	e_x
2	1000	16.9	1000	13.4	1000	15.9	1000	20.1	1000	13.1
3	952	16.7	899	13.8	935	15.9	1000	19.1	910	13.4
4	945	15.8	862	13.4	891	15.7	1000	18.1	821	13.8
5	938	14.9	836	12.8	886	14.8	993	17.3	786	13.3
6	924	14.2	815	12.1	886	13.8	987	16.4	776	12.5
7	924	13.2	806	11.3	875	12.9	987	15.4	765	11.7
8	924	12.2	791	10.5	865	12.1	987	14.4	765	10.7
9	869	11.9	750	10.0	789	12.2	987	13.4	755	9.8
10	848	11.2	737	9.2	771	11.5	974	12.5	745	8.9
11	834	10.4	710	8.5	751	10.8	948	11.9	730	8.1
12	807	9.2	683	7.8	733	10.1	935	11.0	730	7.1
13	786	8.9	640	7.3	730	9.1	935	10.0	719	6.2
14	766	8.2	606	6.7	716	8.3	935	9.0	699	5.4
15	726	7.6	558	6.2	698	7.5	935	8.0	612	5.1
16	687	7.0	501	5.9	663	6.8	922	7.1	571	4.4
17	647	6.4	483	5.1	651	5.9	870	6.5	546	3.6
18	627	5.6	461	4.3	625	5.2	831	5.8	480	3.0
19	548	5.3	380	4.1	557	4.7	779	5.2	367	2.8
20	529	4.5	348	3.5	487	4.4	740	4.4	255	2.8
21	499	3.7	314	2.8	416	4.1	727	3.5	204	2.4
22	438	3.2	253	2.3	381	3.4	584	3.2	138	2.3
23	399	2.4	197	1.9	340	2.7	494	2.7	112	1.7
24	279	2.3	98	2.3	232	2.7	377	2.4	82	1.1
25	179	2.3	76	1.8	191	2.2	260	2.2	41	0.7
26	110	2.4	62	1.1	150	1.7	221	1.5	10	0.5
27	80	2.1	28	0.7	85	1.5	130	1.2	0	—
28	70	1.4	7	0.5	38	1.8	52	1.2		
29	60	0.5	0	—	21	1.9	39	0.5		
30	0	—			12	2.0	0	—		
31					12	1.0				
32					3	1.5				
33					3	0.5				
34					0	—				

Survival is high in the first fifteen months of life after which there is a rapid decline and most animals are dead after about two years. This decline in the population and its relevance to physiological and ecological factors is discussed later on.

Comparisons of populations of this sort are more meaningful if expressed in terms of the expectation of further life (e_x) at any given moment of time. In continuously reproducing species such a comparison can give a measure of the relative contribution each population may make to the total number of larvae produced and

TABLE III

Ascidia nigra; *expectation of further life* (e_x) *in various populations in relation to density and time of settlement. A to F are the principal populations used in the present study, and L.S. (D), (E) and (F) are late settlers in the main populations. M is a population studied in an earlier experiment* (cf. *Goodbody, 1962*)

Population	Settlement date	No. animals	Density/sq m	e_x
A	Oct. 59	145	129	16.9
B	Dec. 59	464	414	13.4
C	Feb. 60	228	204	—
D	April 60	341	304	15.9
E	June 60	77	69	20.1
F	Aug. 60	196	175	13.1
M	Aug. 57	327	146	12.0
L.S. (D)	Nov. 60	34		9.1
L.S. (E)	Nov. 60	114		10.25
L.S. (F)	Nov. 60	34		11.1

hence to survival of the species. The expectation of life of these populations, of the original study population in 1957 and of three late settled populations in the present study are presented in Table III. If for the time being we exclude the data on late settled populations (L.S.) and examine only the data for the five main populations of 1959/60 and the one for 1957, it is apparent that there is considerable
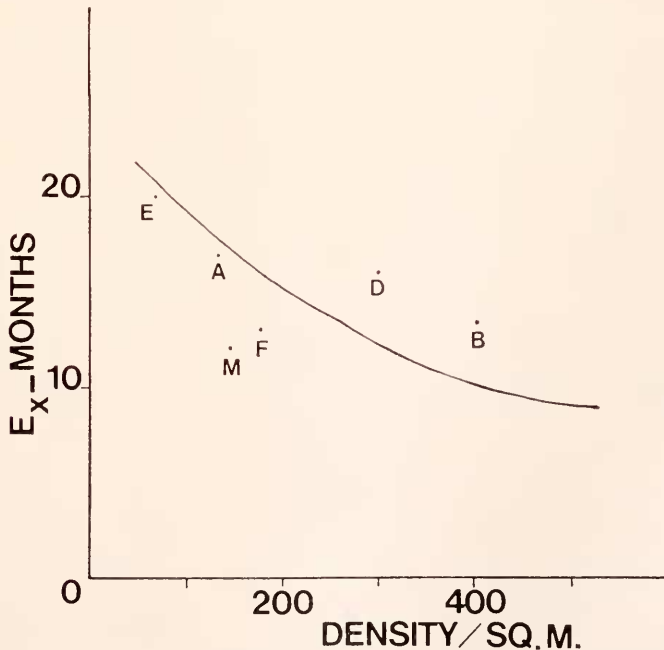

FIGURE 5. Relation between expectation of life (e_x) and density in six populations of *Ascidia nigra* (see text). The line is a trend line and is not calculated.
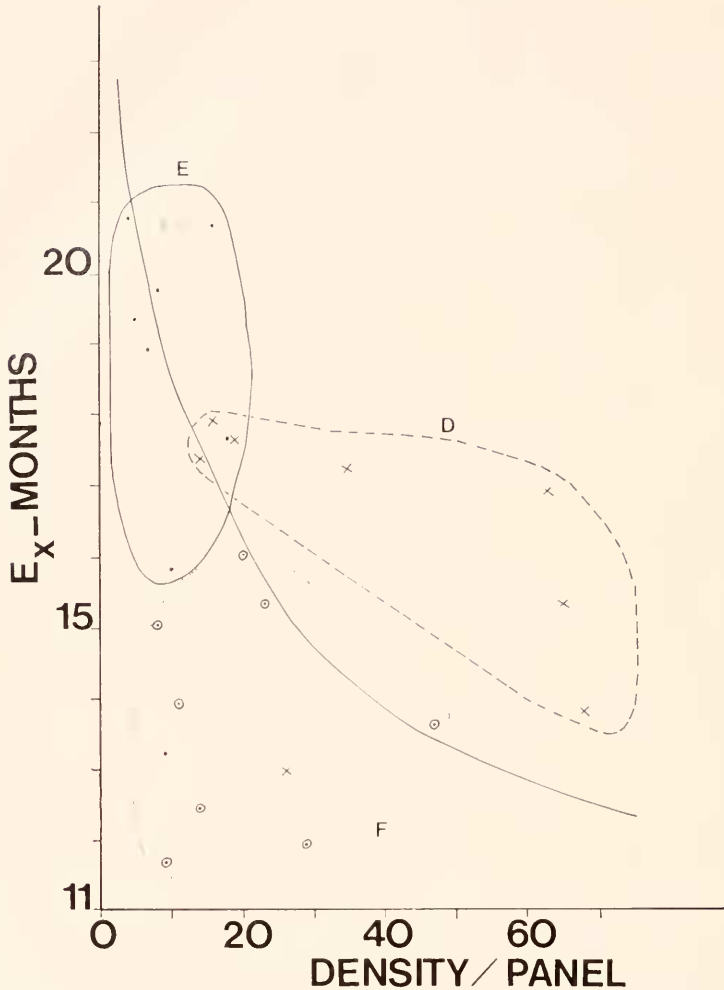
FIGURE 6. Relation between expectation of life (e$_x$) and density in various sub-populations of *Ascidia nigra*. The curved line is a trend line only and is not calculated. Sub-populations belonging to population D (April settlement) are enclosed by a dashed line; populations E (June) is enclosed by a solid line and population F (August) is enclosed by a dotted line (for further explanation see text).

variation in expectation of life between different populations. The data are insufficient on which to draw conclusions concerning seasonal variation, but it is apparent from simple inspection that there may be a relationship between density and expectation of life; this is plotted in Figure 5 and suggests a curvilinear relationship. However, this must be treated with caution as there are many other factors, ecological and physiological, governing mortality.

Each population is in reality composed of a series of sub-populations represented by the eight separate panel surfaces on which the communities are growing.
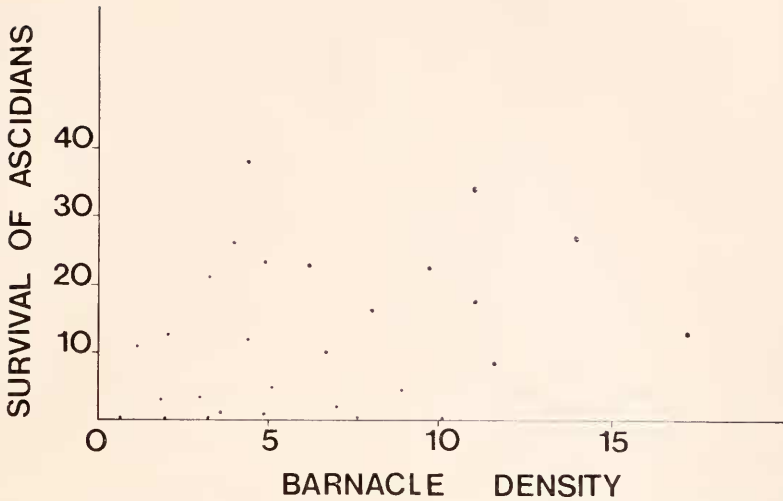
FIGURE 7. Relation between maximum recorded density of barnacles per square centimeter and the survival of ascidians on the twenty-first day after settlement. Survival is expressed as a percentage of the original population (see text).

This enables us to look at density effects in a different way by calculating the expectation of life for each of the sub-populations and plotting these against density. Data for 24 such groupings are plotted graphically in Figure 6. Only data from populations D, E and F are used in this analysis, and no data are drawn from the damaged populations of A and B. There is again a suggestion of a curvilinear relationship but the points are too widely spread for any definite curve to be drawn. This indicates, of course, that factors other than density are operating to control survival and is made clear by drawing lines to enclose the points from each of the main populations, D, E and F which are now seen to occupy separate positions on the plot.

We can then only tentatively conclude that survival and expectation of life are influenced by density but that other forces are modifying or controlling this effect. These are discussed below.

Cause of mortality

Goodbody (1963a) suggested a number of factors which might contribute to mortality in juvenile ascidians but did not identify any one thing which might cause such marked differences between populations as are illustrated by the data presented in this paper. He suggested that competition from barnacles and interference by growths of filametous algae might be important factors as well as overgrowth by colonial ascidians.

In the present study records were kept in the first year of the changes in populations of barnacles and the growth of filamentous algae but there is no evidence at all that either of these was contributing in an important way to changes in survivorship of ascidans. Since maximum settlement and activity of barnacles occurs between the 7th, and 14th days after immersion of a panel we have examined the

TABLE IV

Suspended matter in the sea at Port Royal, 1965. Measurements are in milligrams per liter (Gibson, 1967)

Month	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. of Observations	5	8	9	5	9	8	7	8	6
Mean	4.6	4.9	4.3	5.3	5.4	5.75	4.3	4.9	6.85
S.D.	1.7	0.9	1.6	0.6	0.85	1.53	2.5	1.48	4.78

relationship between ascidian survival at the 21st day and the maximum density of barnacles occurring in the community (Figure 7). It is apparent that high densities of barnacles cannot be held responsible for high mortality in certain ascidian populations. On the contrary there is an indication that there might be a direct relationship between high survival of ascidians and high densities (*i.e.,* high survival) of barnacles, although if this is true the relationship is obscured by other modifying factors.

Similarly if survivorship is plotted against growth of *Enteromorpha flexuosa,* the dominant filamentous algae, there is no apparent correlation at all (see Gibson, 1967, for further details). It seems therefore that while the presence of barnacles and filamentous algae may contribute to ascidian mortality by modifying the environment, neither is of sufficient importance to account for the wide fluctuation in survivorship so frequently observed. However, while we were studying these populations it became apparent that there was another variable which might be of
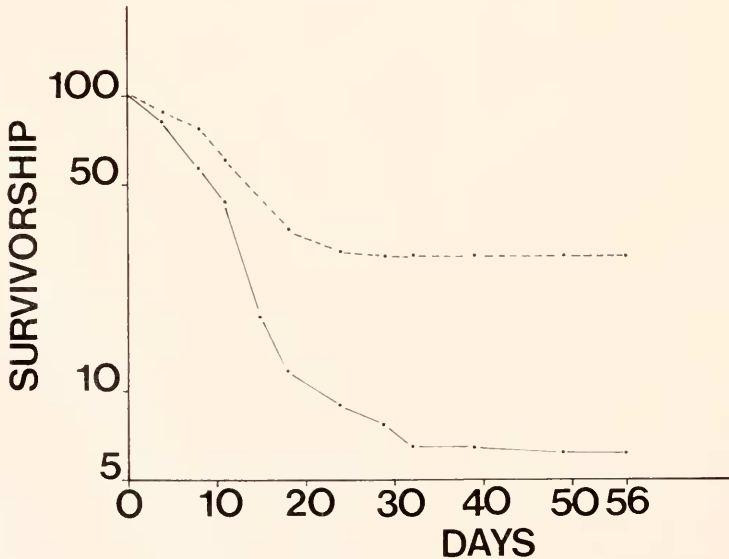

FIGURE 8. Survival of hooded (broken line) and unhooded (solid line) populations of *Ascidia nigra* during the first eight weeks of life, when reared at four feet (1.2 meters) below the sea surface.

more importance than any of those previously considered, and this was the accumulation of particulate matter and benthic diatoms in such a way as to produce a blanketing effect on the whole community.

On the basis of 65 observations, made between April and December 1965, Gibson (1967) showed that the quantity of suspended material in the sea off Port Royal varied from 0.5 to 16.3 mg/liter. In the absence of data on the composition of this material and the nutritional requirements of *Ascidia nigra* it is impossible to say how this might affect survival. The mean monthly values shown by Gibson and reproduced in Table IV do not indicate any trend that might account for changes in survival. Nevertheless observation has shown that at times large quantities of material accumulate on communities and that considerable growths of diatoms notably *Licmophora, Diatoma* and *Baccilaria* are associated with these deposits, the whole appearing as a "blanket" on the community.

The significance of these accumulations became apparent too late to enable quantitative measurements to be made in the present study. However Gibson (1967) carried out some experiments in which populations of young ascidians were grown in the normal way on glass slides but in which the whole frame holding the slides was protected by a black leucite (perspex) hood. The effect of this is of course to cut down the available light and reduce algal growth. Two effects were noted in these experiments. The development of the blanket of diatoms and other material was strongly inhibited in comparison to replicate populations growing unshielded, and similarly survival was better in the populations shielded by a hood than in those which were unshielded.
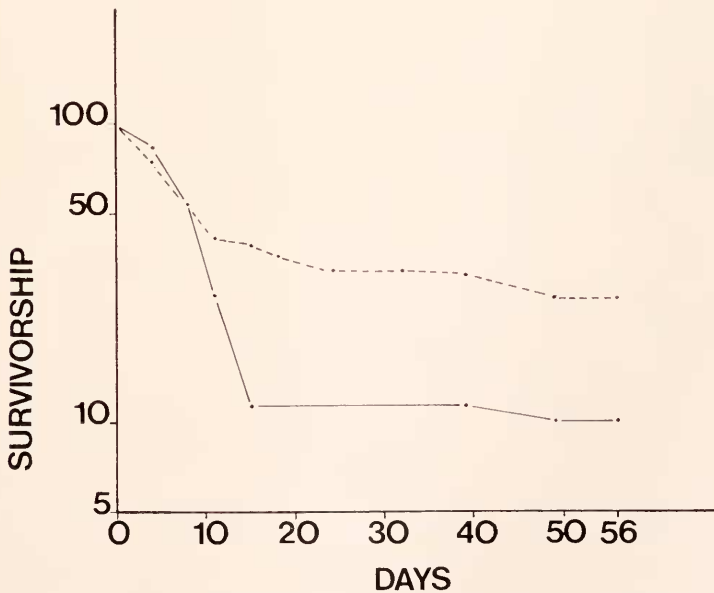

FIGURE 9. Survival of hooded (broken line) and unhooded (solid line) populations of *Ascidia nigra* during the first eight weeks of life when reared at eight feet (2.4 meters) below the sea surface.

Only two such replicate populations have been studied, one at 8 feet and the other at 4 feet below the surface. Survival curves for these pairs are shown in Figures 8 and 9 and show clearly the type of effect which was observed. The data are too few from which to draw meaningful conclusions and we have not been able to follow up this interesting line of approach. However, the data do suggest that large accumulations of benthic diatoms may be an important factor in controlling ascidian populations at this stage of their life and research toward substantiating this and elucidating the factors which control these diatom populations is very desirable.

Ascidians which survive beyond the first few weeks of juvenile life have a high expectation of further life and in the absence of predators it is not easy at first to see what may cause the decline of populations after the first 15 to 20 months of life. In an earlier paper (Goodbody, 1962) the possibility of senescence and physiological death in ascidians was discussed and attention drawn to the fact that in all cases studied ascidians appeared to have a limited life span and that this might be governed by physiological factors. However the decline in the population of *Ascidia nigra* was shown to coincide with the development of the climax sessile community, notably the development of sponges. There are thus three major possible components of mortality in ascidian populations: (1) Physiological death or senescence; (2) Intra-specific competition and (3) Inter-specific competition.

Senescence implies that given ideal environmental conditions and freedom from competition an animal will ultimately die of old age and that there is a maximum age beyond which an individual is unlikely to survive. Senescence in animals has been discussed by Comfort (1956). It is difficult to prove in wild populations where environmental stresses are modifying the life span in various ways. It could be studied in ascidians in aquaria provided an adequate food supply was available. It has not been possible to maintain *Ascidia nigra* in a healthy condition in the aquarium as it appears to be dependent on phytoplankton for its food supply. However the related species *A. interrupta* grows fairly freely in the aquarium and two populations were maintained in large wooden troughs for the whole of their life span, free from competition from other organisms. A steady stream of fresh sea water pumped directly from the sea was maintained through the troughs and appeared to provide adequate food. These populations, derived from artificial fertilizations were set up for another purpose and apart from initial counts no record is available of deaths in the first ten months of life of one population and five months of the other. Nevertheless it is possible to draw survival curves for these two populations and to demonstrate that each has a negative skew similar to those in Figure 4, one lasting for 950 days, the other for 770 days. However since both populations died at about the same time, in spite of commencing life five months apart, there is a suspicion that other factors besides senescence may have been involved. For the time being therefore we cannot be certain that senescence occurs in tropical ascidians and further effort must be directed towards this end.

Intra-specific competition among adult ascidians is also difficult to assess. The data presented earlier suggest that survivorship may be affected by density and if this is correct, presumably it must be due to direct competition for food in densely crowded populations. However crowding may in certain circumstances be beneficial by preventing the growth of other competing species. This point is discussed further below.

The most important factor limiting survival of *Ascidia nigra* appears to be the growth of the surrounding sessile community and particularly the competing effects of sponges and bivalves. In the very early stages of community development *A. nigra* is associated with colonial species of ascidian and sometimes solitary stolidobranch ascidians both Styelids and Pyurids, but there is no evidence at all that these compete for food. They do compete for space and in early development fast growing colonial didemnids may overgrow and smother the solitary forms (Goodbody, 1963a).

The period of ascidian dominance in the community lasts for approximately twelve months after which bivalves and sponges become increasingly important as filter feeders and therefore increasingly competitive with the ascidians. The first twelve months of stability is followed by a decline in ascidians as the sponges and bivalves reach their climax. It is not possible to assess the relative importance of sponges and bivalves as competitors, but it is easy to visualize why sponges are so successful. In a filtering ascidian the area of collection of food is restricted to a small zone around the branchial siphon while in a sponge food collection is a direct function of the surface area. Provided an ascidian can maintain its siphonal collecting zone beyond the limit of sponge growth it may survive, but once the sponge grows beyond this it is likely to "trap" and filter all water in the neighborhood (Goodbody, 1962).

During the course of these investigations detailed notes and photographs were kept of the monthly changes taking place in the communities. In order to assess the impact of the climax sponge community on life expectation in ascidians the populations D, E and F have been examined to see what difference, if any, occurred between populations. On the basis of their expectation of life we should expect that the climax may have been reached more quickly in F ($e_x = 13.1$) than in D ($e_x = 15.9$) which should be more rapid than E ($e_x = 20.1$). The detailed analysis is too bulky to reproduce here but may be summarized as follows. In D sponges had penetrated noticeably by month 6 (M6), were common by M10 and dominant by M15 to M16. In E sponge had penetrated by M6, was not considered significant until M11 but did not fully take control until M19; they never became so common as in D and F. In F sponge had penetrated by M4, was common by M8 and had a dominant foothold by M11/12.

It would seem that survival in E may have been enhanced by the relatively slow development of sponge but suppressed in F by the early and extensive growth of sponge. In D sponge developed at about the same time as in F but the much greater density of ascidians made expansion more difficult and perhaps served a protective function. We thus have an anomalous situation in which a high density of ascidians may be a disadvantage in terms of intra-specific competition but may also be an advantage in staving off the competition of sponges and even bivalves. In the case of population D the growth of solitary ascidians consisted of dense aggregations of both *A. nigra* and Stolidobranch ascidians of several species which between them left little space for sponge colonization and development.

DISCUSSION

Data presented in this paper confirm that survivorship in the first two months of life is exceedingly variable and may range from zero to 33% of the original

population of settled larvae. This variability is not markedly seasonal but it is possible to identify two periods of exceptionally poor survival, one centered around June and the other around September. The mid-summer period is of particular interest as it has previously been demonstrated that natural settlement is minimal at this period (Goodbody, 1961a, 1965) and unpublished data on gonadial cycles suggest that reproductive activity as a whole is depressed between April and July. However, this lead cannot be pursued any further until far more is known about spawning cycles. We have not been able to ascertain for certain what are the causes of mortality in this "critical period" after metamorphosis but predation, smothering by fast growing colonial ascidians and interference by filamentous algae and excessive blankets of diatoms and fine particulate material appear all to be important factors. Blankets of diatoms have also been found to be an important cause of mortality in the temperate water ascidian *Corella willmeriana* (Lambert, 1968), and they may explain the differences between survival of young ascidians at 8 feet and at 4 feet below the surface. Similar environmental factors must be operating at both levels as periods of good survival at 8 feet are normally matched by periods of good survival at 4 feet, but in general more than twice as many animals survive to two months of age at 8 feet as at 4 feet. The water at Port Royal is heavily laden with suspended material and light penetration is poor. The mean of 14 secchi disc readings taken over a period of one year was 4.2 meters ($\pm$ 1.44 meters). Such a value suggests that the difference in illumination may be sufficient to cause significant differences in diatom growth at the two levels of our panels, 1.2 meters and 2.4 meters.

It is obvious that food supply might also be limiting on certain occasions but at present we have no data at all on the particular nutritional requirements of young ascidians. Nevertheless, it is unlikely that food *per se* is ever limiting, as the water is so heavily laden with suspended material, but the availability of this food might be affected by interference from other organisms preventing a free flow to the ascidian. Alternatively, turbulence might cause the ascidian to close its siphons repeatedly and halt the filtration process. These are effects which at present we cannot measure.

Once the black pigment is developed mortality decreases sharply and from the fourth week onward populations remain fairly stable for about a year (Goodbody, 1962 and present paper). This stability can be attributed to a lack of predation and relative freedom from competition. Apparently the test substance is distasteful (Goodbody, 1962) and hence the freedom from predation. In dense aggregations of *Ascidia nigra* intra-specfic competition may be important and result in a density dependent relationship. Competition between different species of ascidian has not been studied. We know (Goodbody, 1967) that within the genus *Ascidia* there is sufficient ecological isolation to prevent competition, but the effect of dense aggregations of stolidobranch ascidians such as *Pyura vittata* and *Microcosmus exasperatus* on less specilized forms such as *Ascidia nigra* is unknown. There is nothing in the present study to suggest competition between the two except for space, but studies on the feeding ecology of these forms would help to clarify the issue.

The major influence on populations of adult *Ascidia nigra* still seems to be the developing communities of sponges and bivalves which reach dominance, if not their

climax, about fifteen months after a new community has started to develop. Although sponge communities are known to act as inhibitors to the development of sessile communities (Goodbody, 1961b) their effect on adult ascidian populations is most likely direct competition for food as suggested earlier in this paper. Furthermore this competitive exclusion is apparently confined to the less specialized phlebobranchiate ascidians such as *A. nigra* and stolidobranchs continue to thrive in amongst the sponge communities. When the communities discussed in this paper were finally removed after three years there were stolidobranch ascidians still living there. This is a reflection of the difference in branchial structure and hence ability to filter the water (Croxall, 1971).

The effect of sponges is demonstrated more clearly if we examine all of the data in Table II where the populations of late settling *Ascidia nigra* are compared in terms of their expectation of life with the original populations amongst which they have settled. These late populations are derived from a total of 182 new animals which settled in the populations D, E and F in October and November 1960 as the result of unusually high survival of young ascidians in established communities. All of the late settled populations have a considerably shorter expectation of life than the originals but the two populations (early and late settled) have tended to die at about the same time. We interpret this as being due to the effect of the surrounding community.

There remains the question of senescence. Clearly under natural conditions few specimens of *Ascidia nigra* have an opportunity to grow old but are excluded by competition much earlier. The longest survival in these experiments was an animal which lived for 33 months as against a mean expectation of life for all populations of 15.9 months. In the laboratory study of the related species *A. interrupta* the longest survival was 900 days (about 30 months) and in spite of the uncertainty in that study, it seems that three years is likely to be the maximum longevity obtainable in these animals.

Comparable data to show the expectation of life in other species of ascidian are not available, but there is ample evidence to show that amongst solitary forms a life span of between one and two years is the general rule, irrespective of latitude (Table V). *Corella willmeriana* is an exception which appears to live for no more than eight months (Lambert, 1968). It is probably also true that solitary ascidians are in general primary colonizers and poor competitors in the face of more efficient filter feeders such as bivalves and sponges. However, the potential for exploiting the environment in this way is considerably greater in tropical than in temperate water species. Tropical species are able to reproduce throughout the year and hence larvae are always available and able to exploit new situations, but in higher latitudes breeding seasons are restricted (Millar, 1971) so that larvae are only available for a few months of the year, when many other organisms are also competing for space.

Deevey (1947) predicted that marine species of animals having pelagic eggs and larvae should exhibit positively skew rectangular survival curves in which there is extremely high mortality beginning in early life, but the few individuals which survive to advanced ages have a relatively high expectation of further life. Our data confirm that this is likely true for *Ascidia nigra*, although we do not have data for the pelagic phase itself. Data given in this paper show that on average

Species	Locality	Life-span	Reference
Ciona intestinalis	Scotland	1–1½ years	Millar, 1952
	Sweden	1 year	Dybern, 1965
	Venice	1 year	Sabbadin, 1957
	Mediterranean	2 years	Pérès, 1946
Ascidia mentula	Norway	3 years	Dybern, 1969a
Ascidia nigra	Jamaica	2–3 years	Present work
Ascidia interrupta	Jamaica	2–3 years	Present work
Ascidiella aspersa	Scotland	1–1½ years	Millar, 1952
	Norway	2–3 years	Dybern, 1969a
Ascidiella scabra	Baltic	12–14 months	Dybern, 1969b
Chelyosoma macleayanum	Alaska	4 years	Huntsman, 1921
Chelyosoma productum	British Columbia	3 years	Huntsman, 1921
Chelyosoma columbianum	British Columbia	1 year	Huntsman, 1921
Corella parallelogramma	Norway	1 year	Dybern, 1969a
Corella willmeriana	Washington	3–8 months	Lambert, 1968
Dendrodoa grossularia	Britain	1½–2 years	Millar, 1954
Styela coriacea	Baltic	1½–2 years	Diehl, 1957
Styela plicata	Venice	1 year	Sabbadin, 1957
Molgula manhattensis	Venice	1 year	Sabbadin, 1957

only 6.6% of metamorphosing larvae survive to eight weeks of age. It is likely that survival in the pelagic phase, which lasts for only a day, is even less. Figure 10 has been drawn on the assumption that 0.5% of fertile eggs ultimately reach the stage of settlement and metamorphosis, but even if that estimate is grossly incorrect it will make little difference to the fact that the overall survival is as predicted by Deevey (1947).

There are still relatively few other data on survivorship in marine invertebrates. Hatton (1938) and Connell (1961) have both illustrated life table data for barnacles; Sutherland (1970) has studied the dynamics of populations of the limpet *Acmaea scabra* and Frank (1965) *Acmaea digitalis*. These are all intertidal organisms and the environmental stresses on populations are therefore totally different to those in *Ascidia*. Walne (1961) showed that oysters (*Ostrea edulis*) living at the low water mark of spring tides in Wales exhibit a positively skew survival curve but the life span is about twelve years and the period of heavy mortality lasts throughout the first eighteen months of life after which the mortality rate is very low. This type of survival curve is very similar to that of *Ascidia* although the time scale is completely different. Paine (1963) has analyzed the dynamics of populations of the brachiopod *Glottidia pyramidata* in Western Florida. *Glottidia* is a benthic filter feeder living in sand bars consolidated by marine grasses. Unlike *Ascidia* the pelagic larval life lasts for about three weeks and Paine has made quantitative estimates to show that there is in fact a massive mortality in this phase of the life history. However, the subsequent survival curve approximates to Deevey's (1947) diagonal type thus suggesting that there is a constant loss from the population rather than a stable population which dies quite suddenly as appears to be the case in *Ascidia*.

Figure 10 illustrates the differences between these two animals by showing Paine's original survival curve for *Glottidia* and a composite survival curve for *Ascidia nigra*. The latter curve is based on population E in the present study for adult animals and uses a mean survival of 6.6% for the juvenile phase in the first two months; it also assumes a survival of only 0.5% in the pelagic phase. This latter figure has no basis in fact and is used merely to complete the graph. The actual value for survival in the pelagic phase is unimportant for comparative purposes and a difference of one order of magnitude would not alter the picture illustrated. The important point is that once the pelagic phase is complete the patterns of survival in the two animals are quite different and probably reflect differences in the type of mortality affecting the two species. *Glottidia* is actively preyed upon
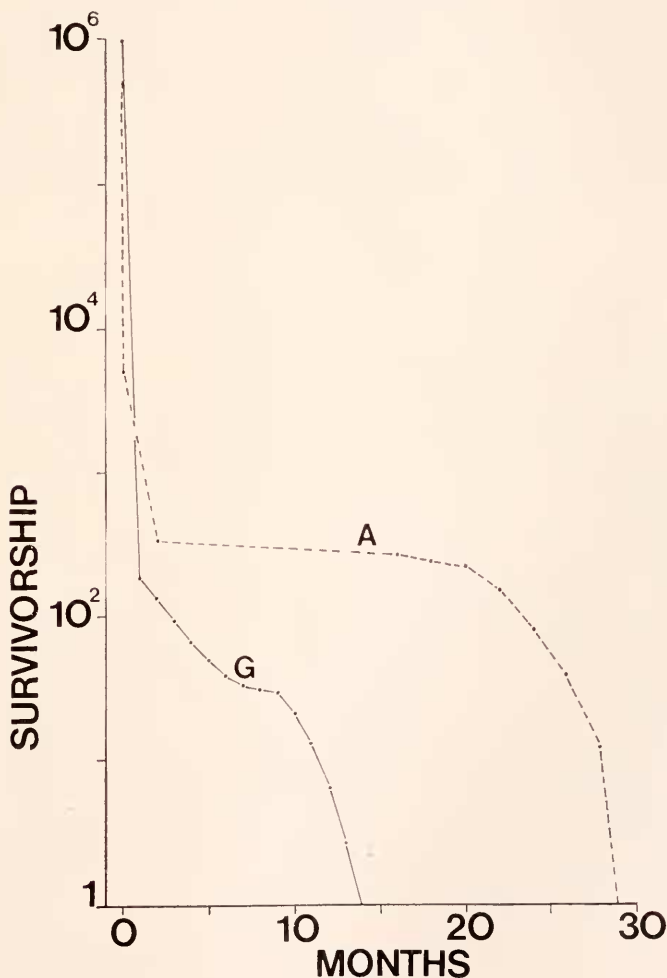

FIGURE 10. Survivorship curves for *Ascidia nigra* (Jamaica) (A), and the brachiopod *Glottidia pyramidata* (Florida) (G). Data for the pelagic phase of *Ascidia* are assumed, the remainder of the data taken from the present work. Data for *Glottidia* are from Paine (1963).

by birds and perhaps by other organisms and there appears to be an almost constant percentage loss from the population regardless of size. *Ascidia,* like *Ostrea,* appears to have no important predators in adult life and the population remains stable until near the end of its life when, as suggested earlier, the competitive action of other species brings about the onset of death. It is possible that *Ascidia* and *Ostrea* may be unusual in this respect and that the majority of marine invertebrates have life tables similar to *Glottidia,* but data are needed on many more species before positive conclusions can be drawn.

Summary

1. The survival of populations of juvenile ascidians in the first two months of life, and adults of two months and older has been studied on a seasonal basis in Jamaica, West Indies.

2. The greatest mortality takes place during the first three weeks of life during which period animals growing at eight feet (2.4 meters) have a significantly better survival than those at four feet (1.2 meters).

3. Seasonal differences in the survival of juvenile populations are not pronounced but periods of poor survival are centered around June and September. Outside of these months survivorship is very variable but similar patterns of change occur at depths of four feet and eight feet.

4. Survival and expectation of life of adults are not affected by the season of the year but are affected by density and by growth of the associated biota.

5. The blanketing effect of populations of diatoms and detritus may be a major cause of mortality in juvenile ascidians. Interference by barnacles and filamentous algae is apparently of little importance.

6. Death of adult populations is usually coincident with the time at which sponges grow level with the inhalent siphon of the ascidian and it is suggested that there is a direct competition for food between the two organisms.

7. The overall pattern of survival of *Ascidia* is discussed in relation to other animals and particularly to the branchiopod *Glottidia.* The life table of *Ascidia* may be unusual as a result of low predation in adult life.

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